This situation is well exemplified by the *punctatus* group as here seen. A definition can be proposed but there will be multiple exceptions to certain characters, and certain fringe species which could as well be included or excluded.

A tentative definition (with exceptions) follows: Species of moderate size (but *nigrolineatus* is rather small, and *laevis* relatively large). The snout is produced either by bony structure, swelling, or soft proboscis. The color is probably green in life (usually purples and blues in alcohol), perhaps an exception in *nigrolineatus*. The ear is small and rather ventrally placed (on the level of mouth). The nostril is separated by a single prenasal scale from the rostral. The head scales are flat, pavimentose (even in *boulengeri*, which has keeled ventrals and keeling of the dorsal scales). The loreal rows are few (as few as two in *laevis*, as many as seven in *punctatus*. There are no or only a few scales between the supraorbital semicircles (0–2). The interparietal, larger than the ear, is of moderate size (large in *laevis*, *dissimilis* and *proboscis*) and separated from the semicircles by 0 to 4 scales. Suboculars broadly in contact with supralabials. Mental deep, not wide (widest in *nigrolineatus*). Well developed sublabials present. Dewlap large, scales in rows narrowly separated by naked skin (scales *not* in rows in *proboscis*). Middorsals not or not appreciably larger than flank scales (a dorsal crest in *proboscis*). Ventrals smooth (keeled in *boulengeri* which, however, intergrades with smooth-scaled *punctatus*), squarish, transverse. Tail more or less compressed with double row of scales dorsally (a single crest in *dissimilis* and *proboscis*).

This is an extensive list of similarities. However, the differences between species, emphasized above by the exceptions, are as striking as the similarities. They are of many sorts and it is natural to inquire whether the differences are less important than the common characters. It will be useful, therefore, to examine the differences in some detail.

1. *Snout differences.* *A. nigrolineatus* is in this regard not very different from many anoles not closely related to it: the bony structure of the snout itself has been stretched into a tapering, bluntly pointed structure. *A. dissimilis* carries the condition of *nigrolineatus* to an extreme. In contrast, the bony snout of *A. punctatus* is very little modified, but the rostral scale is swollen, protuberant. *A. laevis* has this scale produced into a broad-based flexible appendage. *A. phyllorhinus* has a narrow flexible appendage *above* the triangular rostral scale, this appendage having small granular scales. *A. proboscis* is very similar in the general conformation of the area but the scales on the flexible proboscis are

elongate. The differences here imply, as we have already suggested, that no single linear series can be envisioned; at least two are required. It is, however, possible to suppose that there has been radiation from a central type — perhaps *punctatus*, perhaps an ancestor of *punctatus*.

2. *Interparietal size.* The interparietal is large and in direct contact with the semicircles in so many species of diverse relationships, and the interparietal may so often differ in size and in distance from the semicircles in closely related species that this character is probably of minimal systematic value above the species or superspecies level.

3. *Dewlap squamation.* Again a character subject to much parallel modification and often different within a superspecies. *A. proboscis* is anomalous among the compared species in having a rather uniform squamation of the dewlap rather than scales in distinct, separated rows, but this is probably of no major significance.

4. *Dorsal crest. A. proboscis* is again very peculiar in having a dorsal crest of strongly enlarged sub-triangular scales. Such a crest is known in several West Indian so-called giant anoles but is very unusual in mainland species. It does, however, occur in some Guatemalan *A. pentaprion* — whether as an anomaly or a population character is unknown. Special though this feature seems in *A. proboscis*, it is hard to regard this as more significant than the extraordinary proboscis — so like that of *phyllorhinus* in which there is no hint of a dorsal crest.

5. *Tail.* The difference between a tail with two rows of scales dorsally and one with a pronounced single crest is a very obvious one. Schmidt (1939), in describing *Anolis barkeri*, and also Myers and Carvalho (1945), in describing *A. phyllorhinus*, have made much of the double-rowed condition — a feature which does appear to be unusual in anoles. There is usually in *Anolis* only a single row, whether or not this is produced into a crest. The systematic value of the double row is, however, much diminished by just the case in which Schmidt first used it: *A. barkeri* is a Mexican species which on osteological grounds (Etheridge, 1959) belongs to a very different section of the genus from the South American species in which this peculiarity is otherwise known.

In my judgment these differences, though disturbing at first glance, do not provide serious difficulty for a concept which unites all these species as a unit group. There are strong cross resemblances between species that on other characters would be separated. Thus, *dissimilis* shares with *proboscis* the character,

unusual in South America, of a crested tail, but in the nasal appendage and snout structure *proboscis* resembles *phyllorhinus* and is very different from *dissimilis*.

More awkward for the desiderate goal of taxonomic clarity are the species I have described as "fringe species." These are: *transversalis* (including *buckleyi*); the *solitarius-tigrinus* superspecies; *jacare*.

All of these have a double row of scales dorsally on the tail, all have smooth ventrals, few loreal rows, pavimentose dorsal head scales, few or no rows between the supraorbital semicircles, suboculars broadly in contact with supralabials, mental deep, not wide, well developed sublabials.

However, the ear is rather large, the color is complex with much cross-barring and spotting. The species of the *solitarius-tigrinus* series are all of small size (40–50 mm snout-vent length), *jacare* and *transversalis* are of moderate size. One peculiar feature which unites this set of species but is untrue or unknown for all those I have referred to the *punctatus* group (untrue for *punctatus*, unknown for the others) is the presence of black pigment in the female dewlap, and its absence in the male structure (which is also somewhat better developed).

To include these species in the *punctatus* group would seem to enlarge it too much; yet a considerable degree of affinity seems probable.

An evolutionary perspective for the *punctatus* group

The first described proboscis anoles — *A. laevis* Cope (Rio Huallaga, Peru) and *A. phyllorhinus* Myers and Carvalho (lower Rio Madeira, Brasil) were Amazonian. This is also true of *A. dissimilis* (on the upper Rio Madre de Dios). But *A. proboscis* Peters is from Pichincha Province in Ecuador, west of the Andean water shed, and *A. nigrolineatus* is from the Pacific lowlands near Guayaquil. *A. punctatus* — the central species of this putative complex — is much more widespread than any of the other species occurring in Amazonia, the Guianas and the forests of eastern Brasil, but neither it nor its western race (with keeled ventrals) — *boulengeri* — ever transgresses into the Trans-Andean Province.

There is, thus, in this species group — if it is a reality — no special geographic pattern except that of being clearly and wholly South American.

That this group is part of a wider autochthonous South American section of *Anolis* has been demonstrated by Richard Etheridge (1959). The species of the *punctatus* group, all examined radiographically by him, and a wider circle of forms which include such

species as *boettgeri, chloris, fasciatus, fraseri, frenatus, insignis, jacare, latifrons, microtus, mirus, nasofrontalis, peraccae, pseudotigrinus, solitarius, squamulatus, tigrinus, transversalis, ventrimaculatus,* are all characterized by possession of posterior caudal vertebrae without transverse processes and without autotomy septa, by the possession of four parasternal chevrons attached to the ribs and by having the lateral arms of the interclavicle divergent from the proximal parts of the clavicles. This is an assemblage of characters that Etheridge has demonstrated to be quite distinctive, and geographically quite coherent, occurring in species of mainland South America (but not those of the West Indies or Malpelo Island) and also in two or three species — *frenatus, insignis* and *microtus* — present in extreme southern Central America.

This is a very varied series in everything but these distinctive skeletal characters. These anoles are very different in size (including both dwarfs and giants), and in squamation (Table 2). The series, therefore, has every appearance of being an old assemblage which has had the time to diversify and which has exploited its opportunities.

The autochthonous South American section of *Anolis* shares South America with a group clearly not autochthonous but with its stronghold and center of origin to the north in Central America and Mexico. Though the latter group is clearly an invader from the north, it has reached every part of the total range of *Anolis* in South America. It is amazing that the ranges of these two groups of divergent history should be so closely coterminous in mainland South America.

This invader group is distinguished on Etheridge's osteological characters by having caudal vertebrae *with* caudal autotomy septa, *with* transverse processes which are inclined forward, and *with* an interclavicle the lateral arms of which are in contact with the clavicles. Osteologically, therefore, they are quite distinct from the old South American anoles. In squamation, as Table 2 shows, there is broad overlap. It is, therefore, impossible on external characters to make a separation of the two groups. Indeed, species belonging to the two groups have sometimes been confused with one another, and, in other cases, while the species characters permit ready separation, it will still be impossible *on externals* to allocate the species to group other than randomly.

Yet in bias and trend the two groups do differ. This too is shown in Table 2. In toe lamellae the bias of the alpha group is to higher numbers, that of the beta group to lower numbers. This character

(and probably more obscurely some of the others) is a reflection of an ecological bias in the two groups: the alpha group includes more deep forest, highly arboreal species, the beta group more species of open country — ground, grassland, or bush.

In ecology, as in so much else, there is strong overlap, but the bias or trend is clear. At the extreme of the beta series is an anole that actually lives in or at least takes refuge in holes in the ground (Ruthven, 1922), that in fact has abandoned wholly its arboreal heritage and with it the clinging hairs on the toe lamellae so characteristic of all other anoles. This anole, though only the extreme of its series, is customarily placed in a distinct genus; it is *Tropidodactylus onca*.

At the opposing extreme in the alpha series are probably to be placed the proboscis anoles — which again might be placed in a genus apart did they not seem to achieve their distinctive rostral structure in different ways. Neighbors to these in the extreme wing of the alpha series are *punctatus* and, if I interpret matters rightly, the two new species that are described in this paper.

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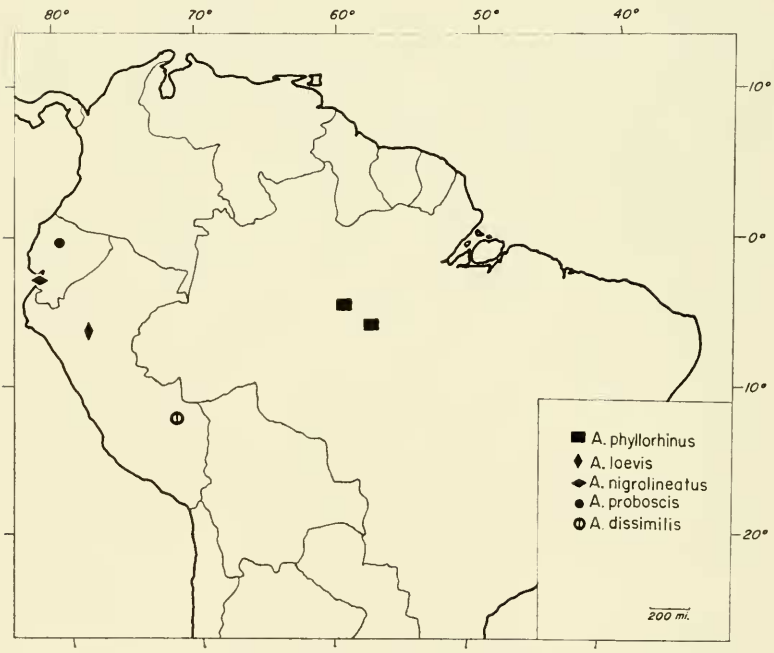

Fig. 3. Map of the distribution of *punctatus* group anoles except *A. punctatus* itself. The exact limits of the latter's very wide range are not known.

Table 1
Scale characters of *punctatus* group anoles

	punctatus Daudin 1802	*laevis* Cope 1875	*phyllorhinus* Myers & Carvalho 1945	*proboscis* Peters & Orcès 1956	*dissimilis* n. sp.	*nigrolineatus* n. sp.
proboscis	rostral swollen in ♂	soft protuberance covered with small scales (only ♂ known)	leaf-like, laterally compressed with granular scales (only ♂ known)	leaf-like, laterally compressed with elongate scales (only ♂ known)	no modification of snout (only ♂ known)	no modification of snout (only ♂ known)
scales between second canthals	11	4 (Cope)[1]	10	9	8	6
scales between semicircles	0–2	0	0	1	0	1–2
scales between interparietal and semicircles	2–4	0	1–2	2	0–1	3
temporals > or < dorsals	<	> (Cope)	=	<	<	=
loreals	4–7	2	4–5	4	4–5	5–7
suboculars in contact with supralabials	+	+	+	+	+	+
labials to center of eye	6–10	?	6–7	9	11	11

[1] Much of the information on *laevis* must come from Cope's original description. Although the type (ANSP 11368) is still in existence, it is in such poor condition that very little can be learned from it. However, the type confirms that there does exist a proboscis anole clearly different from those known by satisfactory material.

Table 1 — Continued
Scale characters of *punctatus* group anoles

	punctatus	*laevis*	*phyllorhinus*	*proboscis*	*dissimilis*	*nigrolineatus*
sublabials in contact with infralabials	2–7	?	5–6	2–3	2–4	2–3
median gular scales in contact with mental between sublabials	3–4	?	4	2	2	3–4
middorsal rows enlarged	0	0	0	1 (irregular crest)	gr	(gr)
tail crest	double row, no crest	double row, no crest	double row, no crest	+	+	double row, no crest
ventrals [1]	sti	stj	sti	sti	soj	st(i)
lamellae 4th toe	24–30	?	25–26	19	17	18
toe expansion	wide	narrow	wide	wide	wide	wide

[1] s = smooth; i = imbricate (i) subimbricate; j = juxtaposed; t = transverse; o = oblique; gr = middorsal enlarged, grading into flank scales.

Table 2

Character range in South American anoles

	alpha anoles	*beta anoles*
number of toe lamellae	14–30 (mode 18–21)	10-27 (mode 14–18)
scales across snout	4–25	7–20
scales between semicircles	0–5 (7 *)	0–4
dorsal scale rows enlarged	0–2	0–12

* Though several alphas range up to five scales between the supraorbital semicircles, the maximum reported here occurs in two exceptional specimens of *A. princeps* Boulenger (= ? *frenatus* Cope).

Glyphomitrium mittenii (A.Jaeger) Mitt., Trans. Proc. Roy. Soc. Victoria 19: 57 (1882).

Type: Australia, Tasmania, north side of the Cataract, Launceston, on rocks, date unknown, *Archer s.n.*, ? herb. Mitten in NY, not seen.

= *Ptychomitrium serratum* (Mitt.) Hook.f. & Wilson, Fl. Tasman. 181 (1859), synonym *fide* Jaeger (1874) *nom. illeg.* (Art. 53.1), later homonym of *Ptychomitrium serratum* Bruch & Schimp. (1837). Basionym: *Glyphomitrium serratum* Mitt., J. Proc. Linn. Soc., Bot. 4: 73 (1859).

Type: 'On rocks: north side of the Cataract, Launceston, *Archer*'

Plants in dense cushions to about 30 mm tall, in life green to olive above (becoming yellow-green to yellow-brown in herbarium specimens), reddish brown to black below; leaves moderately crisped when dry, spreading widely when moist. Leaves lingulate-subulate from an ovate base, mostly 2.2–3.2 mm × 0.6–0.8 mm, plicate, apex acute; margins usually weakly recurved in the lower half, coarsely serrate towards the apex (occasionally ± entire), bistratose to tristratose in the upper part of the leaf; lamina usually irregularly bistratose in longitudinal rows or patches in the upper leaf; costa strong, failing just below the apex; cells arranged in regular longitudinal rows, in mid-leaf quadrate to shortly rectangular, about 6–8 × 6–11 μm, thick-walled with a rounded lumen, becoming smaller and subquadrate to quadrate towards the apex, much longer and lacking chloroplasts towards the leaf base except at the margins (to about 60 μm long), those in the extreme leaf base usually porose.

Often polysetous. Perichaetial leaves similar to vegetative leaves but slightly smaller. Seta straight, 2.0–5.5 mm long. Capsule erect to slightly inclined; urn oblong-ovoid, 1.0–1.5 mm long; operculum to about 1.1 mm long, conical with a long beak; peristome single, of 16 finely and densely papillose teeth split almost to the base into pale to dark pink to orange filiform segments with paler tips; annulus present. Calyptra mitrate, split into lobes all around the base, covering 1/2 to 3/4 of the urn.

Illustrations: Figs 3, 4c, 5c. Also Wilson (in Hooker 1860, plate CLXXIII, figure 3) as *P. serratum*.

Habitat: Grows on rock in shaded situations; also occasionally on coarse-grained soil, and very rarely epiphytic.

Distribution: Tas, Vic, NSW, southern Qld; apparently endemic to south-eastern Australia.

Discussion: This species often grows with *P. acutifolium* or *Holomitrium perichaetiale*, or sometimes both, and can be easily overlooked when dry because the upper margins may be inrolled, hiding the marginal teeth. However, when wet the teeth are easily discernible under a hand lens. As in *P. acutifolium*, the upper leaf lamina in *P. mittenii* is usually bistratose in scattered longitudinal rows or patches. This character has not been reported previously.

Additional specimens examined: AUSTRALIA: Tasmania: Mt Strzelecki, Flinders Island, 20 Oct 1996, *Scott s.n.* (MELU-2754); German Town, 5 km NNW of St Marys, 30 Nov 1988, *Curnow 2452* (CBG-8807819). Victoria: summit of Mount Oberon, Wilsons Promontory, 6 Apr 1994, *Meagher 0159* (MELU s.n.); Snowy River Gorge, Apr 1969, *Ashton s.n.* (MELU-7357B). New South Wales: Bains Gully, 3 km south of Majors Creek, 25 Apr 1983, *Streimann 27653* (CBG-8305729); Pipers Lookout, South East Forests National Park, 5 Sept 2012, *Karunajeewa s.n.* (MEL-2364217A). Queensland: Mt Maroon, 4 Oct 1974, *Streimann 372* (CBG-51236).

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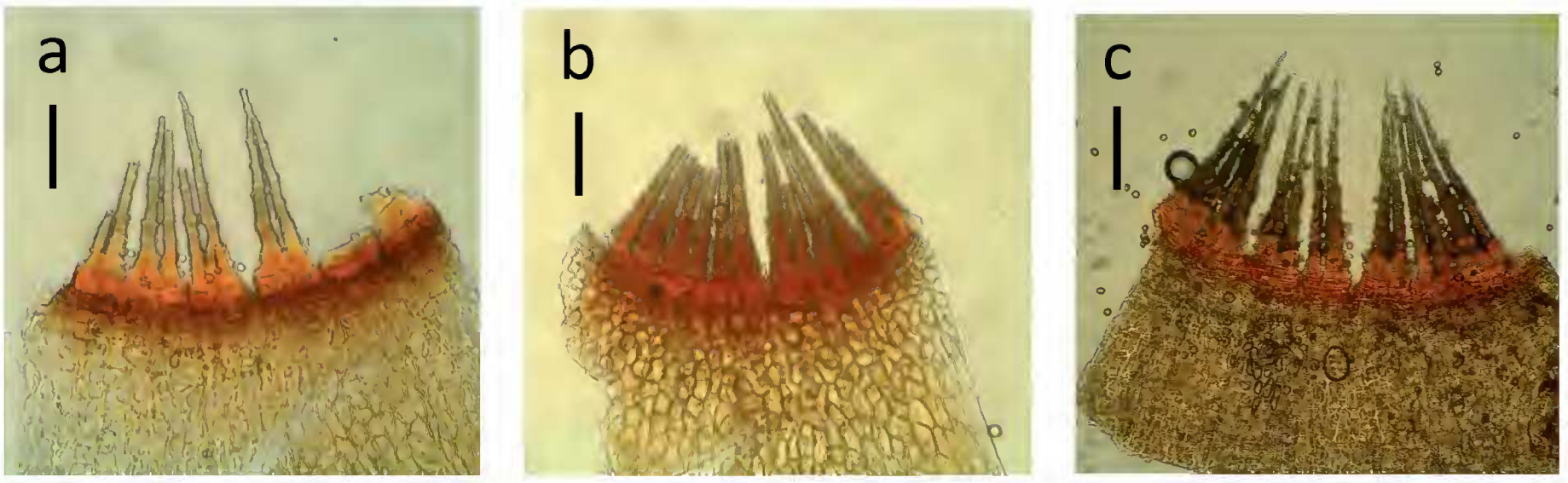

Fig. 4. Partial peristomes: **a**, *P. acutifolium* (*Meagher LH-128*); **b**, *P. australe* (*Scott s.n.*, MELU-1741); **c**, *P. mittenii* (*Scott s.n.*, MELU-2754). Scale bars: 100 µm.

Fig. 5. a, *P. acutifolium* (*Scott s.n.*, MUCV-1274, herbarium specimen); **b**, *P. australe* (*Meagher LH-348B*); **c**, *P. mittenii* (*Meagher 0159*, MELU, herbarium specimen). Scale bars: 5 mm.

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